they are valueless as age indicators, or else they are of very recent formation.

The changes here indicated need not for the present affect the ages of minerals back to the Paleozoic. In the Paleozoic we should consider carefully the stage of alteration of the mineral. In pre-Cambrian minerals we may well be skeptical of the very old ones which have had to undergo the effects of many varied geologic changes.

Fortunately we have some independent checks on the lead method of computing the ages of minerals. Bradley, from a study of varves is able to extrapolate a figure for the length of the Eocene which harmonizes with that deduced by the lead method, as Schuchert has pointed out. Of course this cannot be extrapolated very far, but with further study of all the different methods of estimating geologic time we may hope for better general agreement on the main features of the problem.

SUMMARY

Some reasons are given for ascribing more weight to thorium minerals as age indicators than they have heretofore received. In uranothorites, it was argued, the lead isotopes would not be separated by leaching, so that a loss of uranium would have to be postulated to bring the RaG/U and ThD/Th ratios in agreement.

BOTANY.—*Sex and accessory cell fusions in the Uredineae.*[1]

C. F. Andrus,[2] Bureau of Plant Industry. (Communicated by L. L. Harter.)

INTRODUCTION

A number of contributions have been made to the study of fertilization in the Uredineae (1) (2) (3) (10) (15) since the writer (4) first published evidence that spermatium nuclei enter the tips of superficial hyphae and migrate to the haploid cells of the aecial primordia. The new contributions have chiefly corroborated the observation that spermatium nuclei enter the exposed gametophytic hyphae. The further progress of the spermatium nuclei and the process by which they eventually become paired with individual nuclei of the aecial primordium has escaped the scrutiny of these observers. Likewise, there is still lacking an adequate interpretation of those cell fusions

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[2] Grateful acknowledgment is made to Dr. L. L. Harter, who has provided facilities for research and advised in the preparation of the manuscript.

and apparently miscellaneous nuclear migrations in the young aecium that are so commonly associated with the act of fertilization.

The writer has recently had occasion to examine a number of slides of the bean rust, *Uromyces appendiculatus* (Pers.) Fries, and the cowpea rust, *U. vignae* Barclay, some of them prepared after the earlier communication was submitted for publication. In a number of instances details of the obscure fertilization process appeared on these slides with unusual clarity and it is believed that these observations are of sufficient interest and value to deserve some record. The new observations will emphasize more strongly that the relation between spermatium and receptive cell in the aecium of Uromyces is a true sperm-egg relation, and will indicate in addition that certain cell fusions which accompany diploidization in the aecium are an important accessory to the fertilization process. In conclusion it is proposed to discuss the possible bearing of the newly observed phenomena of sex and organography in the Uredineae upon the general problem of sex in fungi.

THE ENTRANCE AND MIGRATION OF SPERMATIUM NUCLEI

Attention has been given to a more detailed examination of the means by which spermatium nuclei reach the aecium from their point of entrance at the host epidermis. A first fact worthy of comment is the apparent ease with which the nuclei disregard the numerous crosswalls in their passage through the often intricate maze of mycelial strands. This fact has been verified by the observation that the spermatium nuclei can be made to contrast strongly with the ordinary or indigenous cell nuclei of the gametophytic mycelium and thus can be identified at various points throughout the infected area. Contrast in stain has been obtained with the triple combination of safranin, gentian violet, and orange G on material fixed in Carnoy's and in Fleming's weaker solution.

When revealed by a good differentiation of stain the spermatium nuclei display a curiously compact structure which differs markedly from the structure of the indigenous cell nuclei. Figure 1, C, G, H, I, and L shows this difference in structure and indicates the difference in intensity of stain. The normal or indigenous cell nuclei show reticulation outlined in gentian violet, which is frequently very distinct in the greatly enlarged egg nuclei. A conspicuous nucleolus is invariably present in the (basal cell) nuclei and frequently is equal in diameter to the spermatium nucleus at the time the latter has just entered the basal cell. The nucleoli retain the safranin stain, but often with a pale center giving somewhat the appearance of a vacuole. (Fig. 1, K, *c*.) Spermatium nuclei rarely show reticulation but are stained richly, with gentian violet predominating, and contrast in brilliance with the dull safranin of the egg nucleoli. An eccentric position of the deeply stained portion is a common characteristic of the spermatium nuclei at this stage. The stainable portion is frequently crescent-shaped (fig. 1, J, L) or comma-shaped (fig. 2, C, D); a faint edging or halo (fig. 2, F, *b*) often gives them a curiously detached appearance. The distinctive appearance of the spermatium nuclei is lost during the first conjugate division with egg nuclei.

Having observed the characteristic structure and staining properties of the newly introduced spermatium nuclei, it is possible to observe these bodies in their devious progress through the crosswalls of the trichogenous hyphae and in the act of migrating between adjacent cells of the fertile layer in the aecium. Figure 1, A and B, shows fusion of spermatia with the tips of superficial hyphae. Figure 1, D to F, shows spermatium nuclei in process of migration through hyphal crosswalls. Many such cases have been observed. In Figure 1, G, is shown a spermatium nucleus as it maneuvers past the cell nucleus in its passage through the trichogenous hypha. Spermatium nuclei after they have reached the base of the aecium are shown in Figures 1 and 2. Figures 1, J, K, and 2, A, show migration between continuous and between adjacent cells at the base of the aecium. On certain slides these can be seen with great frequency.

It is necessary to conclude that cell walls furnish remarkably little inconvenience to the movements of nuclei. Whether passage through the walls is secured by dissolution, or by openings normally present, or whether the forces causing the movements of the nuclei are sufficiently potent to cause mechanical rupture, is not entirely apparent from the observations made. From the appearance of the crosswall after passage of the nucleus shown at *e* in Figure 2, I, it would seem

Fig. 1.—Entrance and migration of spermatium nuclei of *Uromyces appendiculatus*, A, E to G, J to M, and *U. vignae*, B to D, H, I. ×1500. A, B.—Fusion of spermatia with gametophytic hyphae. C.—Spermatium nucleus (*a*) contrasted with cell nucleus (*b*). D to F.—Migration of spermatium nuclei (*a*) through crosswalls of trichogenous hyphae; cell nuclei at *b*. G.—Indigenous cell nucleus (*a*) in a conducting hypha allowing a spermatium nucleus (*b*) to maneuver past on its way to the aecium. H.—Contrast of spermatium (*a*) and cell nucleus (*b*). I.—Initial fertilization of a basal cell; spermatium nucleus at *a* and egg nucleus at *b*. J.—Entrance of spermatium nuclei (*a*, *b*, *c*) into basal cells. K.—Entrance of spermatium nuclei (*a*, *b*) into basal cells; the egg nucleolus (*c*) is often similar in size to spermatium nuclei but differs markedly in stain. L.—Early relation of egg (*a*) and spermatium (*b*) nuclei. Note orientation of the egg nucleus as compared to I. M.—Entrance of spermatium nuclei (*a*, *b*) into basal cells. The normal cell nucleus is shown at *c*.

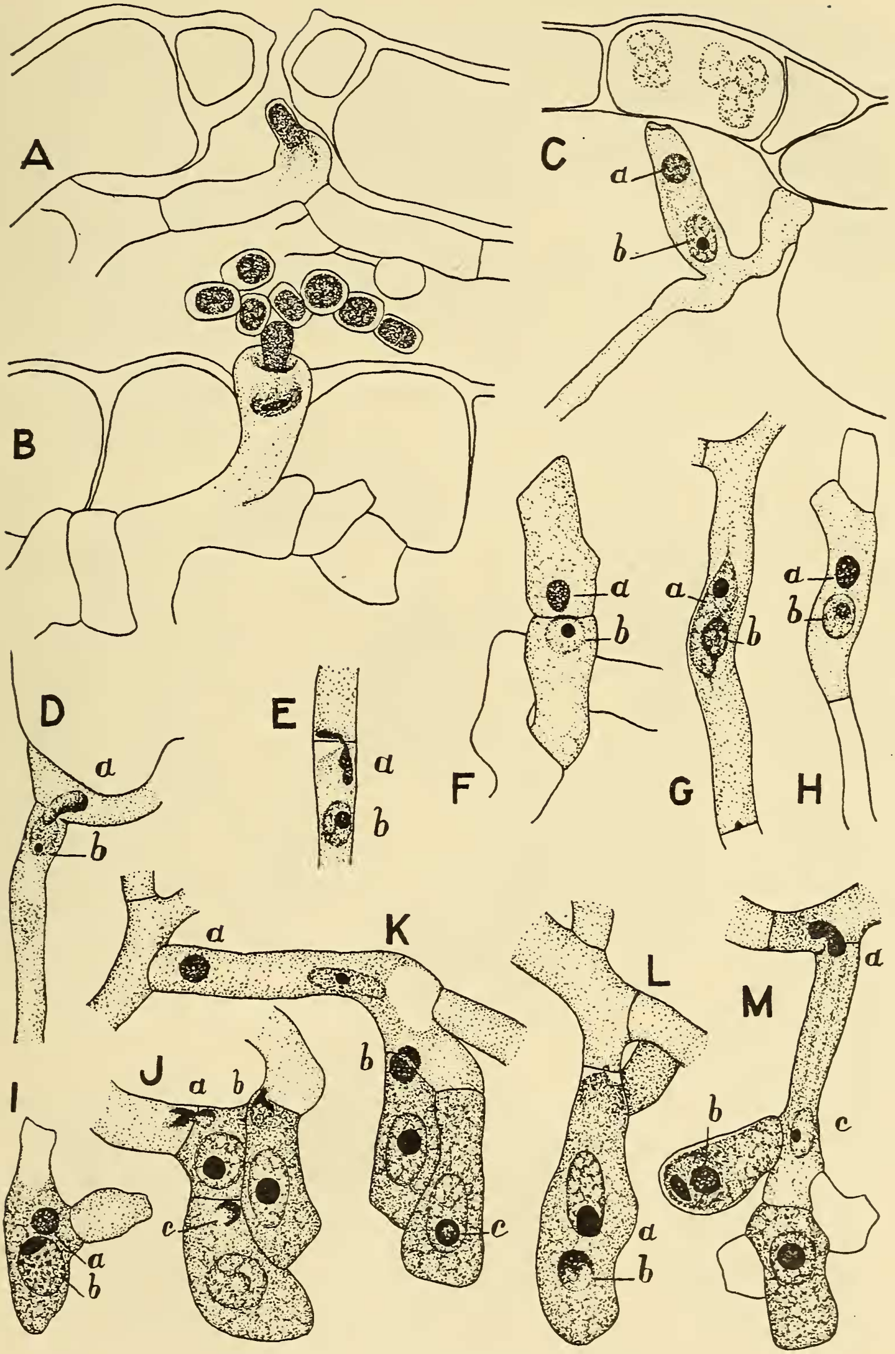

Fig. 1.—For explanation see opposite page.

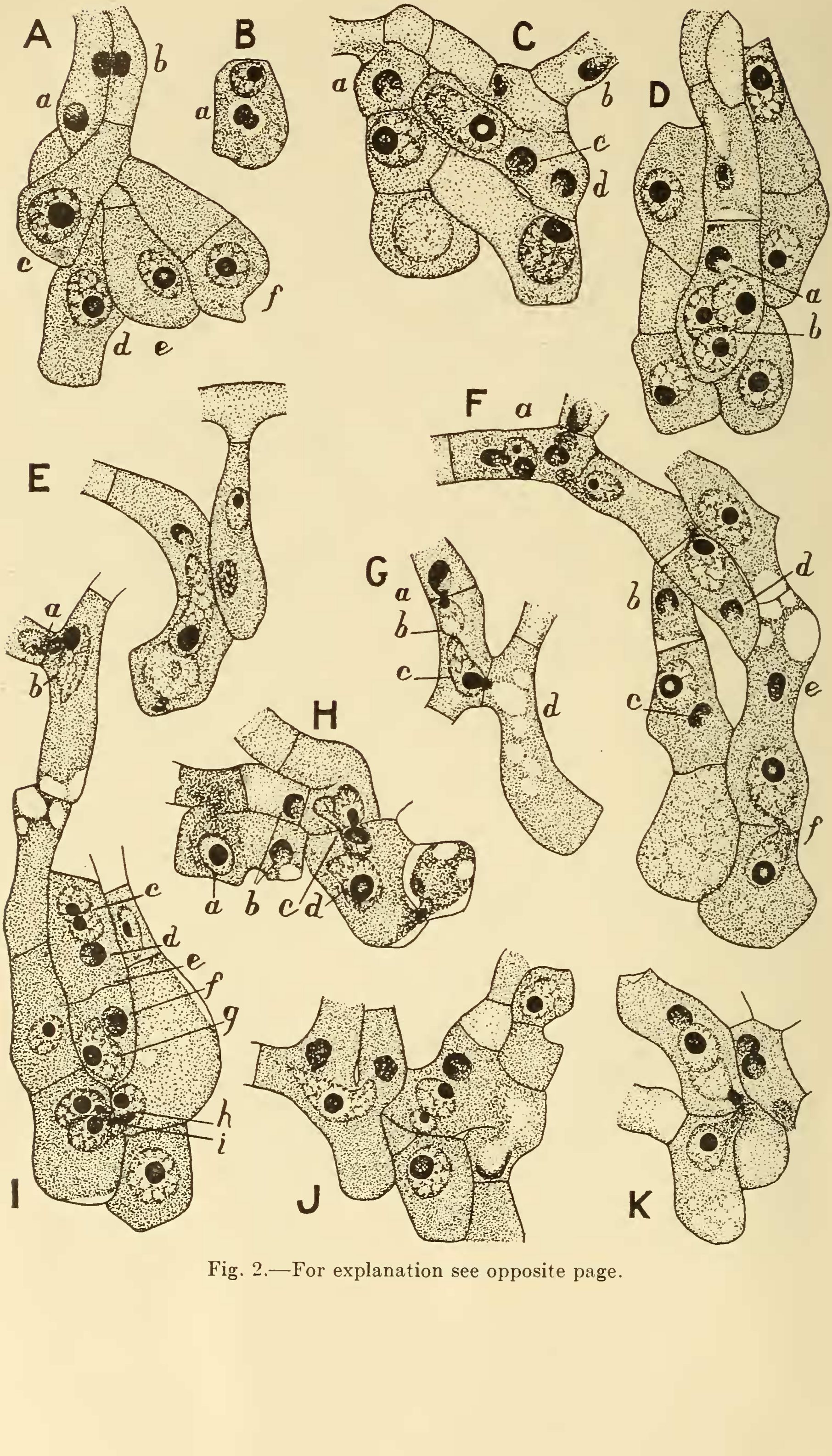

Fig. 2.—For explanation see opposite page.

that the wall has been forcibly ruptured,—less probably dissolved. In Figure 1, M, the nucleus (*a*) is not enough constricted to suggest that its passage is restricted to a small pore. However, Figure 1, E, shows a nucleus much constricted in its passage through the crosswall. Furthermore, it is clear that a pore is commonly present in these hyphal crosswalls, even though it is not certain that the presence of a pore facilitates migration of the nuclei.

It is apparent from the evidence just presented that spermatium nuclei migrate through gametophytic hyphae from the epidermis to the aecium, and these conducting hyphae are still gametophytic after passage of the spermatium nuclei. Up to this point, therefore, the process of fertilization offers little suggestion of any relationship to the diploidization process supposed by Buller (8) to occur in Hymenomycetes.

Allen (1) suggested that in some species of *Puccinia* the aecium may be diploidized by the growth into the aecium of sporophytic hyphae originating near the point of entrance of spermatium nuclei. She even thought she saw some evidence of this on her slides of *P. triticina* Eriks. and *P. coronata* Cda. (2). Such a procedure is conceivable and even probable for such species as *P. caricis* (Schum.) Rebent. where cells of the hymenium are observed to be diploid from their origin (13), but there is no indication that such a method of diploidization may occur even rarely in the bean and cowpea rusts. Aggregations of well differentiated haploid cells are present in definite localized regions of the thallus, and fertilization of these cells is initiated by the entrance of spermatium nuclei. There is no reason to conclude that this is not as true a sperm-egg relation as is to be found in any group of Thallophytes.

ACCESSORY CELL FUSIONS IN THE AECIUM

A further study has been made of the cell fusions and nuclear migra-

Fig. 2.—Nuclear relations in the aecium of *Uromyces appendiculatus*, A, C to K, and *U. vignae*, B. ×1500. A.—Entrance of spermatium nuclei (*a*, *b*) at base of aecium; egg or basal cell nuclei are shown at *c* to *f*. B.—Possible division or fragmentation of a spermatium nucleus (*a*) after it has entered a basal cell. C.—Spermatium nuclei (*a* to *d*) showing evidence of division and migration. D.—Spermatium nucleus (*a*) in a basal cell with 3 egg nuclei (*b*). E.—Migration of an egg nucleus toward an approaching spermatium nucleus. F.—Migration of spermatium nuclei through a series of conducting cells. Note migration of the egg nucleus (*f*) from the terminal cell of the series. A normal cell nucleus is shown at *a* with several spermatium nuclei; spermatium nuclei also at *b* to *d*. G.—Spermatium nucleus (*a*) approached by a normal cell nucleus (*b*) and an egg nucleus (*c*) which has vacated the basal cell (*d*). H.—Nuclear migration at base of aecium; egg nuclei at *a*, *c*, *d*, and spermatium nuclei at *b*. I.—Migration of both spermatium and egg nuclei; spermatium nuclei at *a*, *d*, *f*, and probably *i*; egg nuclei at *b*, *g*, *h*; *c* is probably a recently divided egg nucleus; note ruptured crosswall at *e*. J, K.—Migration of egg nuclei after entrance of spermatium nuclei.

tions that occur within the aecium immediately following the first stage of fertilization. It appears that the fertilization process does not cease with the entrance of a particular spermatium nucleus into a particular egg cell; there occur divisions of the egg nuclei and probably also of the spermatium nuclei, which are followed by further migrations of both spermatium and egg nuclei. As a result numerous originally uninucleate cells are diploidized following entrance of only a few spermatium nuclei. Some suggestion of this was made in an earlier publication (4). It is believed to be possible that in the accessory cell fusions and nuclear migrations there may be found a process in some degree comparable to the diploidization in Hymenomycetes.

It is necessary to distinguish at least two types of cell fusion in the aecia of *Uromyces*, fusions that are undoubtedly stimulated by the entrance of spermatium nuclei, and fusions that occur in aged sterile aecia showing evidence of degeneration. Fusions of the second type, in their advanced stages, involve an almost general dissolution of cell walls accompanied by a multiplicity of small nuclei, often inadequately stained. Allen (2) illustrates fusions of this type for *Puccinia coronata*. They occur regularly in unfertilized infections of bean rust. Migrations of nuclei through small openings are characteristically absent from such material. Initial stages in degeneration of sterile aecia may show fusions that are not clearly distinguishable from fusions that accompany fertilization. It may be stated generally, however, that cell fusions in a sterile aecium involve a general disorganization of cell partitions, whereas fusions associated with fertilization involve nuclear migrations with only local dissolution or rupture of cell walls.

The explanation of cell fusions associated with fertilization in bean and cowpea rusts is then largely a problem of interpreting the nuclear migrations that accompany or follow entrance of spermatium nuclei into the aecium. It appears that the nuclear migrations involve movements of both spermatium and egg nuclei. The difficulty in deciding this point is increased by the fact that spermatium nuclei no longer show the characteristic structure and stain after the first conjugate division. Consequently many of the migrating nuclei which appear to have the structure of an egg nucleus may in fact be of spermatial origin.

Material fixed at an early stage in fertilization will frequently show basal cells with a very nearly ideal relation of egg and spermatium nuclei. Such a one is shown in Figure 1, I. So far as could be determined this is the first spermatium nucleus to enter this aecium. The figure is drawn from a 16 day infection fixed very soon after spermatia were transferred on the surface of the host leaf. The figure certainly suggests a typical sperm-egg relationship, comparable, for example, to the fertilization of an egg in the archegonium of a fern. Figure 1, L, is only a little less convincing in this respect. Of possible significance is the apparent shift in position of the egg nucleolus, which in this case corresponds to the relative position of the spermatium nucleus in the two figures. Fertilization, however, is not ordinarily so simple as would be indicated by these two figures. There is evidence that the spermatium nuclei may divide soon after entering the first basal cell, as appears to be the case in Figure 2, B. The division, if it is such, would appear to be amitotic. Figure 2, A (*b*), may represent such a division occurring at the cell partition. Also the two distinct spermatium nuclei (*c*, *d*) represented in Figure 2, C, may have entered separately but quite as probably are the result of a nuclear division.

The egg nucleus also appears frequently to undergo division, just preceding or immediately following entrance of the spermatium nucleus. That the first divisions of spermatium and egg nuclei are not simultaneous is evidenced by Figure 2, B, as well as *a* and *f* of Figure 3, A. The migration into an adjacent basal cell of one portion of a recently divided spermatium nucleus is suggested in Figure 2, I, although again it should be stated that the spermatium nuclei shown (*d* and *f*) may be of separate origin. That egg nuclei also migrate from cell to cell during this period is evidenced in Figures 2 and 3.

The presence of 2, 3, and occasionally 4, egg nuclei in a single basal cell is a common observation at an early stage in fertilization. The explanation would appear to be that the approach of spermatium nuclei is a stimulus that promotes movement of egg nuclei. This is suggested in Figure 2, G, where the egg nucleus (*c*) has completely vacated the basal cell (*d*) and entered the conducting hypha where the smaller cell nucleus (*b*) already appears to be assisting the approaching spermatium nucleus (*a*) through the narrow aperture in the crosswall. Also in Figure 2, F, where the approach of several spermatium nuclei appears to have exerted some force upon the nucleus in the most terminal unfertilized cell. Again in Figure 2, E, and H to K, and Figure 3, A, migrations of egg nuclei are occurring at several points, but usually in a direction toward spermatium nuclei. Curiously the 2 egg nuclei in Figure 3, B, appear undecided which way to move. Not all instances of this sort lend themselves to interpretation.

The movement of egg nuclei toward the approaching spermatium nuclei may be due to a definite attraction between the two kinds of bodies or it may be merely incidental to a general cytoplasmic movement which has the effect of concentrating the active protoplasmic substances in the fertile layer of the aecium. A general cytoplasmic movement toward the fertile layer would result in the withdrawal of nutritive materials from the sterile portion of the aecium and likewise

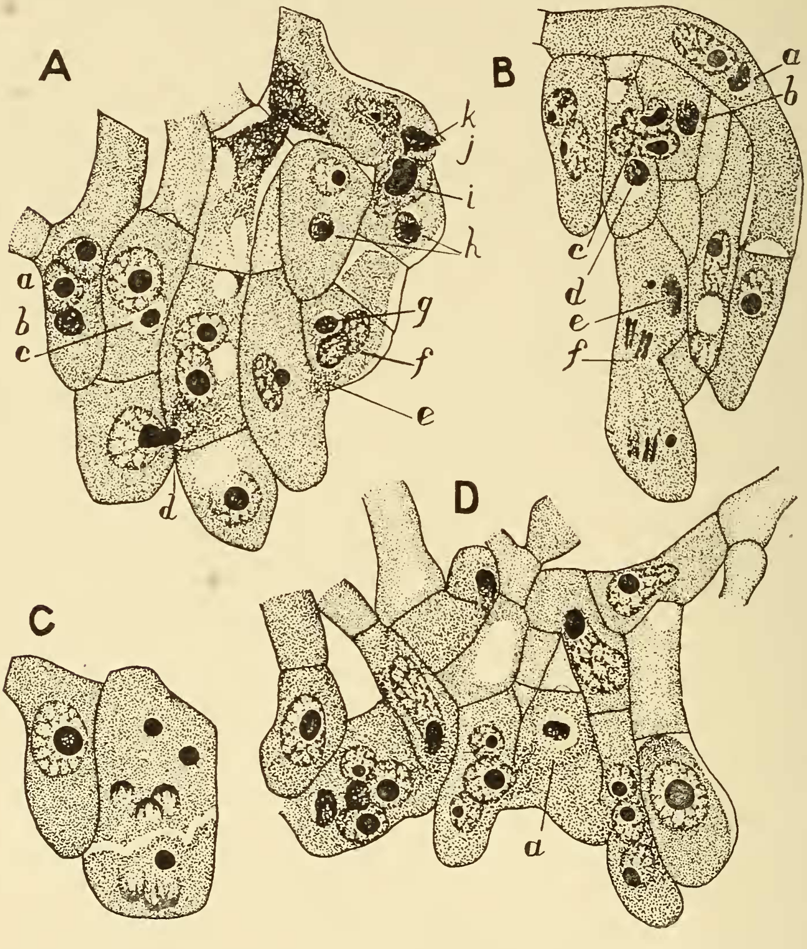

Fig. 3.—Nuclear division and migration in *Uromyces appendiculatus*, A, B, D, and *U. vignae*, C. ×1500. A.—Recently divided egg nuclei at *a* and *f*; spermatium nuclei at *b*, *c*, *g*, *h*, and *k*; cell fusions at *d*, *e*, and *j*; egg nucleolus at *i*; migration at *d* may involve either a spermatium or an egg nucleus. B.—Migration of egg nuclei at *c*; spermatium nuclei shown at *a*, *b*, *d*, and *e*; the conjugate division at *f* probably involves only egg nuclei. C.—Division of a trinucleate basal cell. D.—Cell fusions with evidence of nuclear migrations at several points. An adjacent section shows an egg nucleus and a second spermatium nucleus in the cell at *a*.

might conceivably draw spermatium nuclei from the peripheral hyphae toward the aecium. Whatever may be the force causing migration of egg nuclei from an unfertilized cell into a fertilized cell, such migration would appear to have a nutritive effect and would support later proliferation of the multinucleate basal cell. The cell fusions and nuclear migrations observed in the aecium of *Uromyces* obviously correspond to those described by Blackman (6) and Christman (9) for numerous species of Uredineae; and, although they are not gametic fusions in the sense proposed by the above authors, they do appear to be an important and perhaps characteristic accompaniment of the sexual act.

Migration of egg nuclei is frequently from an unfertilized cell into a cell which has just received or is about to receive a spermatium nucleus. This in certain instances accounts for the multinucleate condition of newly fertilized cells. (Fig. 2, D, I, and K.) In other instances (fig. 3, A and D) the multinuclear condition is probably the result of nuclear divisions that occur previous to the familiar conjugate divisions. Upon this basis it cannot always be inferred that two nuclei in a binucleate basal cell are necessarily of separate origin or of different sex. It is probable that the conjugate division shown in Figure 2, B, involves nuclei neither one of which is of spermatial origin. Later divisions of this basal cell would probably involve the spermatium nucleus shown at *e*.

Some observations have been made concerning the fate of the excess nuclei after spore formation is begun. Reduction to the single pair of nuclei that is so characteristic in cells of a mature aecium may be accomplished by any one of four methods. 1. By eliminating the extra nuclei in the first spore abstricted. 2. By migration of extra nuclei into adjacent unfertilized cells. 3. By degeneration of one or more nuclei. 4. By proliferation of the basal cell into two or more spore chains. There is evidence that all four methods are actually followed at various times. Frequently, as in Figure 3, C, a few basal cells continue to produce spores with more than two nuclei.

It is evident from the above that great irregularity characterizes the nuclear behavior in a fertilized rust aecium. The apparently miscellaneous nuclear divisions and migrations have the result, however, of securing the diploidization of numerous basal cells by means of a comparatively few spermatium nuclei. In this procedure there is some suggestion of the diploidization process in Hymenomycetes, where it is supposed (8) that a single nucleus of one sex can diploidize a whole thallus of different sex. In respect to the two species of *Uromyces* here concerned, it would be a mistake to suppose that the whole rust thallus is comparable to the thallus of a Hymenomycete. For here, at least, the whole thallus is not diploidized by the spermatium nuclei, but only definitely differentiated gametic areas of the thallus. Surrounding hyphae serve as conducting channels for spermatium nuclei but remain haploid after passage of the nuclei.

DISCUSSION

The present communication emphasizes the earlier observation (4) that fertilization of a haploid aecium by entrance of spermatium nuclei in *Uromyces* constitutes a true sperm-egg relation. It can scarcely be denied that each gametophyte of *Uromyces* produces organs that not only function as gametes but have some of the morphological peculiarities of the sperm and egg mechanisms of certain more familiar plants. It would be unwise, however, to emphasize any apparent homologies with the sperm-egg mechanisms of any other group of organisms.

Some confusion has resulted from the paradox offered by fungi of this type, wherein a full complement of "sex" organs are present on individuals of both "sexes." A comparable situation has long been familiar to students of flowering plants; but botanists have never looked upon non-compatibility groups of flowering plants as being sexual groups. Sperm and egg mechanisms, as conceived by the writer, are a part of the characteristic organography of particular species and are frequently independent of the physiological condition of individuals in respect to compatibility. This viewpoint seems to be demanded by the newly observed facts of sex segregation and organography in fungi. Many species that would be homothallic in respect to sex organs are in fact heterothallic in respect to sexual compatibility. Furthermore, it is probable that in certain species that appear to be typically homothallic (and self-fertile) the development of fruiting bodies may proceed parthenogenetically or without any reaction between the sperm and egg mechanisms present (5). Such a homothallic species is in fact unisexual.

Dodge (11) has explained in considerable detail how the sexes segregate in the ascus of *Neurospora* so as to form unisexual strains (of heterothallic forms) and bisexual strains (of homothallic forms). He presumes that a unisexual strain consists of individuals that correspond to either sperm-producers or egg-producers, while the bisexual strain consists of individuals that produce both sperm and egg mechanisms. In the case of certain rust fungi and Ascomycetes, mycologists are forced to an embarrassing conclusion, for here the "sexes" (organs) are obviously segregated in the vegetative divisions of the gametophyte while the conditions of maleness and femaleness (the factors for copulability) are segregated in the nuclear divisions in the ascus and in the basidium. Which of the two above relations is actually segregated in the ascus of *Neurospora*? More recent observations on this fungus (12) would seem to indicate that copulability factors are segregated in the ascus and that the strains which, according to Dodge (11), are unisexual are in fact producers of both sperm and egg mechanisms. Uredineae of the *Uromyces* type are similar to *Neurospora* in that respect.

There is some inclination to look upon sex phenomena in the Uredineae as comparable in many respects with the diploidization process in Hymenomycetes as postulated by Buller (8). Undoubtedly there are points of similarity. Buller indicates how, "in a very simple way," a diploid cell can fertilize a haploid cell, and how the diploidization may continue progressively so that a whole haploid mycelium may be diploidized,—presumably by the entrance into one haploid cell of a single nucleus of opposite sex. There is no evidence from Buller's researches that fertilization by a diploid mycelium is not preceded by a type of reduction. Vandendries and Martens (16) have shown that haploid oidia are formed by diploid mycelia of *Pholiota aurivilla* Batsch, and it is conceivable that this may be a common procedure in other Hymenomycetes. Likewise, Brown (7) presents no evidence that haploid cells are not formed by the rust sporophyte immediately preceding fertilization of a gametophytic mycelium of *Puccinia helianthi* Schw. These announcements show the inadequacy of methods of research in this field which do not include a study of cytological phenomena.

On the other hand, there is perhaps nothing remarkable in the fact that a diploid (or binucleate) cell can fertilize a haploid cell, or that fertilization can occur in any combination whatsoever, providing the necessary sexual gradient exists between the nuclei concerned. On the preceding pages there is described what is believed to be such a process taking place in the aecium of *Uromyces*. By means of nuclear division and migration a single spermatium nucleus is sufficient to fertilize numerous basal cells. Diploidization in *Uromyces*, however, is restricted to specially differentiated gametic areas. In this respect, and in other details, it contrasts strongly with the scheme of diploidization outlined by Buller (8), which apparently is based largely upon the cytological work of Lehfeldt (14).

Buller (8) has attempted to draw a fundamental distinction between the processes of fertilization in Hymenomycetes and in higher plants. The cells which become diploid in Hymenomycetes are not egg cells, Buller conceives, for the whole haploid mycelium should be looked upon as a multicellular egg. Likewise, according to this author, the haploid cells (oidia) which frequently initiate fertilization are not sperm cells, for they too are capable of independent growth and of forming a multicellular individual. This is an ingenious theory. At the same time it might as easily be conceived that the fern gametophyte is a multicellular egg, but upon this multicellular individual there are usually developed characteristic structures which bear the relation of sperm and egg mechanisms. This is quite as true of the rust gametophyte. In the fern gametophyte as well as in the fungus gametophyte fertilizations are not restricted to these differentiated structures.

Sperm and egg mechanisms in all their variations may be looked upon as a part of the characteristic organography of particular species. They may be no more male and female than any two other organs of the individual. In many of these species they are a means by which alone diploidization is possible. In other species the cellular anatomy may be such that sexual unions are not restricted to any specially differentiated cells, even though such be present and functional. The new observations on sex in fungi have revealed little concerning the nature of sex, but they have brought into question the arguments of those who seek to place in different categories gametic unions occurring between undifferentiated cells and those occurring between cells differentiated as sperm and egg. Apparently both types of fertilization occur in the rust fungi.

SUMMARY

Continued observations on fertilization in two species of *Uromyces* emphasize the view that the relation between spermatium and haploid basal cell is a true sperm-egg relation.

The structure and staining properties of migrating spermatium nuclei are described and contrasted with those of nuclei in the conducting strands and in basal cells of the aecium. By means of this contrast it is possible to identify spermatium nuclei at various points within the gametophyte thallus.

The fusion of spermatia with superficial hyphae and the passage of the spermatium nuclei through the conducting strands is described in some detail. The trichogenous hyphae remain haploid after passage of the spermatium nuclei.

Cell fusions that occur in sterile (unfertilized) aecia are distinguished from those occurring at the time of fertilization. Fusions of the first type involve a general disorganization of cell partitions while fusions of the second type are incidental to nuclear migration with only local dissolution or rupture of cell walls.

The period of fertilization is accompanied by migrations of both spermatium and egg nuclei, both of which are believed to divide independently during the initial stage. Migration of egg (basal cell) nuclei appears to be related to the approach of spermatium nuclei. A number of significant details in the relations of spermatium and egg nuclei are described.

The nuclear migrations in the aecium are believed to represent a process of diploidization that may be remotely comparable to diploidization in Hymenomycetes.

The discussion covers the possible bearing of sex phenomena in the Uredineae upon the larger problem of sex in Thallophytes.

LITERATURE CITED

1. ALLEN, R. F. *A cytological study of heterothallism in* Puccinia triticina. Jour Agr. Research **44**: 733–754, *illus.* 1932.
2. ALLEN, R. F. *A cytological study of heterothallism in* Puccinia coronata. Jour. Agr. Research **45**: 513–541, *illus.* 1932.
3. ALLEN, R. F. *The spermatia of flax rust,* Melampsora lini. Phytopath. **23**: 487. 1933.
4. ANDRUS, C. F. *The mechanism of sex in* Uromyces appendiculatus *and* U. vignae. Jour. Agr. Research **42**: 559–587, *illus.* 1931.
5. ANDRUS, C. F. and HARTER, L. L. *Morphology of reproduction in* Ceratostomella fimbriata. Jour. Agr. Research **46**: 1059–1079, *illus.* 1933.
6. BLACKMAN, V. H. *On the fertilization, alternation of generations, and general cytology of the Uredineae.* Ann. Bot. [London] **18**: [323]–373, *illus.* 1904.
7. BROWN, A. M. *Diploidization of haploid by diploid mycelium of* Puccinia helianthi *Schw.* Nature **130**: 777, *illus.* 1932.
8. BULLER, A. H. R. *The biological significance of conjugate nuclei in* Coprinus lagopus *and other Hymenomycetes.* Nature **126**: 686–689, *illus.* 1930.
9. CHRISTMAN, A. H. *Sexual reproduction in the rusts.* Bot. Gaz. **39**: [267]–275, *illus.* 1905.
10. CRAIGIE, J. H. *Union of pycniospores and haploid hyphae in* Puccinia helianthi *Schw.* Nature **131**: 25, *illus.* 1933.
11. DODGE, B. O. *Nuclear phenomena associated with heterothallism and homothallism in the Ascomycete* Neurospora. Jour. Agr. Research **35**: 289–305, *illus.* 1927.
12. DODGE, B. O. *The non-sexual and the sexual functions of microconidia of* Neurospora. Bull. Torrey Club **59**: 347–360, *illus.* 1932.
13. KURSANOV, L. *Recherches morphologiques et cytologiques sur les Uredineés.* Bul. Soc. Nat. Moscou (n.s. 1917). **31** (Sect. Biol.): 1–129, *illus.* 1922.
14. LEHFELDT, W. *Über die Entstehung des Paarkermycels bei heterothallischen Basidiomyceten.* Hedwigia **64**: 30–51, *illus.* 1923.
15. PIERSON, R. K. *Fusion of pycniospores with filamentous hyphae in the pycnium of the White Pine blister rust.* Nature **131**: 728–729. 1933.
16. VANDENDRIES, R. and MARTENS, P. *Oïdies haploïdes et diploïdes sur mycelium diploïdes chez* Pholiota aurivilla Batsch. Bull. Cl. Sci. Acad. Roy. Belg. **18**: 468–472, *illus.* 1932.